The Shell Ornament of *Hysteroconcha* and *Hecuba* (Bivalvia): a Test Case for Inferential Functional Morphology

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(Plates 5 to 7; 2 Text figures)

FOR MANY YEARS zoologists have been making functional inferences about the animals that they study, and, in the case of vertebrate zoologists at least, this type of inference has often been made with a fair amount of scientific rigour. But the recent paper by Geist (1966) on the evolution and functional significance of horn-like organs in the mammals convincingly demonstrates that even with such spectacularly developed and common organs as these there is still ample room for subjective interpretation and divergences of opinion. Unfortunately, the tendency in invertebrate studies has been for functional interpretations to be made merely as asides in the course of routine systematic work; at best such interpretations are generally loosely argued, at their worst they may even become selfcontradictory. In the field of invertebrate palaeontology there has recently been a strong resurgence of interest in functional, as opposed to systematic, studies, and in a series of stimulating papers Rudwick (1961, 1964a, 1964b) has outlined a rigorous 'paradigmatic' methodology which enables at least some degree of precision to be reached in such interpretations. Though the method was developed initially for fossil brachiopods, its applications are not restricted to any one group of animals, and its implications are equally broad.

THE PARADIGMATIC METHOD

Briefly, the paradigmatic (or mechanistic) approach may be considered to consist of four logically discrete steps:

1. Perception

The animal structure in question is examined in some detail and compared with our knowledge of the biology of the animal's relatives, living and fossil, and with our knowledge of similar structures in unrelated animal groups. As a result of this comparison it is generally possible to

suggest more than one reasonably plausible function for the structure.

2. Specification

It is now necessary to test these various tentative functional interpretations against the different idealised structural specifications that are relevant to each. It is essential, in so doing, to take account of the limitations imposed by the properties of the materials involved (e. g. bone, muscle or calcium carbonate, etc.), where these factors are significant. One is thus led to the concept of establishing a paradigm for each postulated function. The paradigm is "the structure that would be capable of fulfilling the [postulated] function with the maximal efficiency attainable under the limitations imposed by the nature of the materials" (Rudwick, 1964 a, p. 36).

3. Evaluation

By comparing the observed structure with its paradigm for each postulated function it is possible to get some idea of the degree of efficiency with which the observed structure could have fulfilled each function. As Rudwick (1964a, pp. 36-37) has already stressed, it is most important to note that closeness of approximation of a structure to a given paradigm only measures the degree of possible functional efficiency of the structure for that paradigm; it tells us nothing directly about the probability that the function we are considering is in fact the correct function.

4. Interpretation

Thus far the analysis has been entirely methodological, and therefore relatively objective. However, to choose between several competing paradigmatic analyses inevitably involves a higher degree of subjectivity. It is necessary at this point to digress slightly.

Most animals that have been adequately studied demonstrate a high level of integration between function and structure. Indeed, it was presumably just this that gave rise to the presently popular technique of viewing animals as functional units of the same type as machines. But it has become accepted that in writing of animals in this way the worst crime is to use language that might be construed as teleological in any sense. PITTENDRIGH (1958, p. 394) has pointed out that an animal, just like a machine, is an end-directed mechanism, and that the slightly hysterical attempts of many writers to use nonteleological language are based "on the mistaken view that the efficiency of final causes is necessarily implied by the simple description of an end-directed mechanism" (l. c., p. 393). PITTENDRIGH further maintains that it is wrong to consider, as many of us do, the animal as a system some features of which may, or may not, be adaptive: "the living system," he writes, "is all adaptation insofar as it is organized." In addition, he takes issue with HUXLEY for having called the organism "a bundle of adaptations" because such a statement implies that organisation is an additive phenomenon, and that discrete adaptations can be isolated from the system.

It would seem to be a dangerous procedure, then, to abstract one particular structural feature of an animal, and to attempt to analyse its probable adaptive or functional role, for "the organism's ends" are likely to be often "served in complex ways unamenable to simple description." But presumably PITTENDRIGH would be the first to agree that it is only by initially, and tentatively, treating the organism as a bundle of adaptations, and by attempting to analyse each of these adaptations separately that we are in the end able to piece them all together and approach the task of interpreting the animal as "all adaptation."

Some structures approach their paradigm very closely - for example, the camouflage of many moths and stick insects, if not corresponding 100% with a camouflage paradigm, is certainly very close to it - but it should be obvious that no structure will ever perfectly fulfill its paradigm, for no animal functions at 100% efficiency. Further, in line with the points quoted above, since all structures are an integrated part of the adaptation of the whole organism they are very rarely, if ever, going to be the result of a single steady selective pressure. Commonly we might expect a structure to be selected for more than one specific function and hence to approach several paradigms loosely, and none specifically. Indeed, RUDWICK (1965) has already described a structure (spines on the Jurassic brachiopod Acanthothiris) that he considers to have probably served two discrete functions; and GEIST (1966, p. 192), in writing of the functions of hornlike organs in vertebrates, concludes that "cervid antlers and bovid horns evolved convergently and function as weapons, secondly as guards and thirdly as organs binding opponents together during pushing and wrestling contests."

Assuming, then, that a structure will never completely fulfill its paradigm, in a given instance we are faced with making comparisons between the actual structure, and the structural paradigms of several possible functions. We adopt for this the procedure outlined by RUDWICK (1961) in his introduction of this methodology: whichever paradigm, of several alternatives, is adjudged to be most closely approached by the structure in question, that paradigm is most likely to be the paradigm of the sole correct function, or of the dominant function of several. The other postulated functions may then (subjectively) be considered as close enough to their paradigms to be interpreted as secondary functions, or alternatively, they may be discarded.

It is important to note that it is at this interpretative stage that a paradigmatic analysis reaches its least rigorous point, for there is generally no quantitative way of measuring how closely a structure approaches several alternative paradigms. Hence the choice between such paradigms is certainly subjective, and must depend largely on the preferences and opinions of the writer concerned.

THE QUESTION OF FUNCTIONALITY

The question as to whether all structures must of necessity have a function is, of itself, outside of paradigmatic methodology. But it is a question that cannot be evaded when interpreting animal structures, for the possibility must always be considered that a given structure is in fact non-functional (i. e. non-adaptive). "The living system is all adaptation insofar as it is organized": PITTENDRIGH would thus presumably maintain that all major structures are adaptive, and hence have a function. RUDWICK (1964 a) is primarily concerned with the logical impossibility of proving non-functionality, but he clearly makes the point (pp. 35, 38) that, without prejudice to the correctness or not of a general principle of functionality, unless we initially assume that a given structure is functional "we shall fail even to perceive the evidence on which any functional reconstruction must be based."

However, these two writers' views apart, it is clearly impossible to assert that all structures must be functional, except in a semantically very loose sense, for there are at least two obvious types of morphological structure for which such an assertion would be false:

1. Pleiotropic genetic effects

The pleiotropic effect, whereby one gene locus may give rise to manifold morphological consequences, has long been known. Predictably, most of the cited examples involve Drosophila; for instance, the mutation 'vestigial' in Drosophila acts primarily to reduce the wing size, but it also makes certain bristles erect instead of horizontal, modifies the balancers, and has noticeable effects on the wing muscles, the shape of the spermatheca, the speed of growth, life length and fecundity of the insect (DOBZHANsky, 1941). There is no doubt that pleiotropism is a widespread genetic phenomenon affecting all groups of animals. Human ingenuity is such that, if pushed to it, a discrete function could readily be invented for all the above morphological changes; or, to put it another way, a different selective advantage could be attributed to each of them. But a paradigmatic analysis of any one of these morphological effects would almost certainly be trivial, for they all form part of a stable genotype and cannot meaningfully be treated in isolation. That is not to say that they are not all individually subject to natural selection, for modern evolutionary theory holds that selectively neutral characters are very rare. Rather, it seems probable that, though all the characters of a pleiotropic set may be subject to individual selection, in most cases the selection for the (or for a) dominant character swamps the effects of the others.

The genetic research necessary for recognizing pleiotropism has scarcely been started for many groups of Recent animals, and it is all but impossible that we shall ever be in a position to describe the genome of fossil forms. Hence the most reasonable approach to this problem is presumably to treat well developed structures (such as, say, elephant tusks, or the spines described later in this paper) as truly adaptive, and assume that they are not merely 'side-effects' due to pleiotropism. In the present state of knowledge there appears to be no rigorous way of justifying such decisions; and only experience, or intuition, can help us make them correctly.

2. Vestigial structures

A further example of a non-functional structure is one that is adjudged to have become obsolescent after a fairly long phyletic history. Such vestigial structures are inferred to have been functional, and hence selected for at some former time, though at the present time they appear to have no continuing usefulness.

The paradigmatic interpretation of vestigial structures is also difficult, for they are capable of closely approaching the paradigm of their ancestral function; as examples one might quote the unerupted teeth of the baleen whales, or the rudimentary limbs of some snakes. However, the problem is not as difficult as with pleiotropism, for vestigiality usually leaves some morphological trace – in the case of a fossilised baleen whale jawbone one would certainly be suspicious of the apparent lack of wear on the teeth. Nevertheless, one has no case for insisting a priori that all vestigial structures are always going to be recognisable as such because of their inevitably possessing certain inconsistencies in their morphology; and this is particularly true of fossil animals where only part of the total morphology is preserved. The possibility of vestigiality, then, must always be borne in mind in functional studies.

PHENOTYPIC RESPONSES

The classic types of phenotypic response to the environment, such as an oyster moulding itself to the substrate or the shells of a particular species of mollusc being thinner in sub-saline water, either have an obvious function, or do not require functional interpretation. But GILBERT (1966) has recently described a fascinating and unusual type of phenotypic morphology in the rotifer Brachionus calyciflorus Pallas, 1766. This species normally possesses two pairs of short anterior spines, and a further pair located posteriorly. If B. calyciflorus is kept in cultures of the carnivorous rotifer Asplanchna brightwelli Hudson, 1889, its female parthenogenetic offspring have an additional pair of long posterolateral spines - structures that were completely lacking in the previous generation - and there is also an induced relative elongation of the normal spines. Eggs from mothers grown in the conditioned medium that are transferred to fresh medium immediately after extrusion develop into long spined forms; conversely, eggs from mothers grown in fresh medium and transferred on extrusion to conditioned medium hatch into short spined forms. Successive offspring from the same mother exhibit decreasing spine production. As GILBERT concludes: "the production . . . of extra spines was mediated by a factor released into the medium by Asplanchna, and represents a phenotypic response of undoubted adaptive significance" - long spined Brachionus being far more difficult for Asplanchna to eat.

It is presumably a moot point whether this rather straightforward type of phenotypic response can be expected in animals higher than rotifers, but it is as well to be aware of the existence of such a phenomenon, even if it should presently appear to be confined to one of the lower animal groups. It would seem likely that such a confinement reflects our lack of knowledge of the phenomenon in other phyla, rather than its true absence.

Since a paradigmatic analysis is not concerned with how a particular structure arose, but only with how well adapted it is, phenotypic structures are perfectly amenable to paradigmatic interpretation. However, should it transpire that the phenomenon described above be widespread in different animal groups, there might be a case for some amendment of the present methodology.

SUMMARY

Though it is not possible to maintain the rigour of paradigmatic methodology right through the functional interpretation of animal structures, such a methodology is an essential tool in any closely reasoned functional analysis.

The palaeontologist normally accepts as part of his discipline an almost complete ignorance of the soft-part anatomy and the behaviour patterns of the specific fossils that he studies. Of course, he may make much use of the current biological knowledge of extant relatives of the animal in question, but in many cases such knowledge is appallingly scanty. As with most types of scientific method, the paradigmatic is dependent for its success on its initial data – these need to be both sufficient and of good quality. Palaeontological data are always relatively insufficient in that soft parts are rarely fossilised.

Theoretically the neontologist is in a much stronger position, for he should have a comprehensive knowledge of the anatomy, ecology and ethology of the animal he is studying. But in fact, so little work has been done on many groups of Recent animals, apart from routine systematics, that the neontologist is in almost exactly the same position as the palaeontologist. This is especially so in invertebrate groups, and particularly true of the Mollusca.

Hecuba and Hysteroconcha are two groups of living bivalves about which very little has been published outside of taxonomic information (and even that is scarce). The degree of interest shown in such spectacular shells by early European shell collectors is reflected by the voluminous description of Hysteroconcha in Systema Naturae - in the entire 'Regnum Animale' only Homo sapiens and Apis mellifera (the honey bee) can record a longer entry (Dodge, 1952, p. 87). The demand for specimens of these shells was due mainly to their beauty of form, but their exotic origins and relative scarcity were contributing factors; and even today it is not easy to come by specimens with wholly intact spines. Inevitably, therefore, attention has centred on the aesthetic appeal these shells made, rather than on their scientific significance. It has passed unnoticed that Hysteroconcha, known from the tropical Americas to the Northern Americas, and Hecuba, known from the western Indo-Pacific, have independently acquired the remarkably similar morphological structures that constitute their main attraction from the collectors' point of view.

The unfortunate lack of published data on these shells carries one unexpected advantage – it enables a 'palae-ontological type' of paradigmatic analysis to be carried out with which future observations on the living animal may be compared. Thus this paper may serve as a partial 'test case' of paradigmatic methodology; the amount of light thrown on the functional suggestions made herein by future research on the living animals will be some guide as to the reliability of the methodology, and perhaps tell palaeontologists just how far it is possible to make reasoned inferences from the incomplete data of dead shells.

Hysteroconcha

In most respects Hysteroconcha is a typical member of the Pitarinae (Plate 5, Figure 1), possessing the characteristic dentition, moderately deep pallial sinus and concentric ornament of that group. It differs, however, in the possession of two remarkable sets of spines, one (the

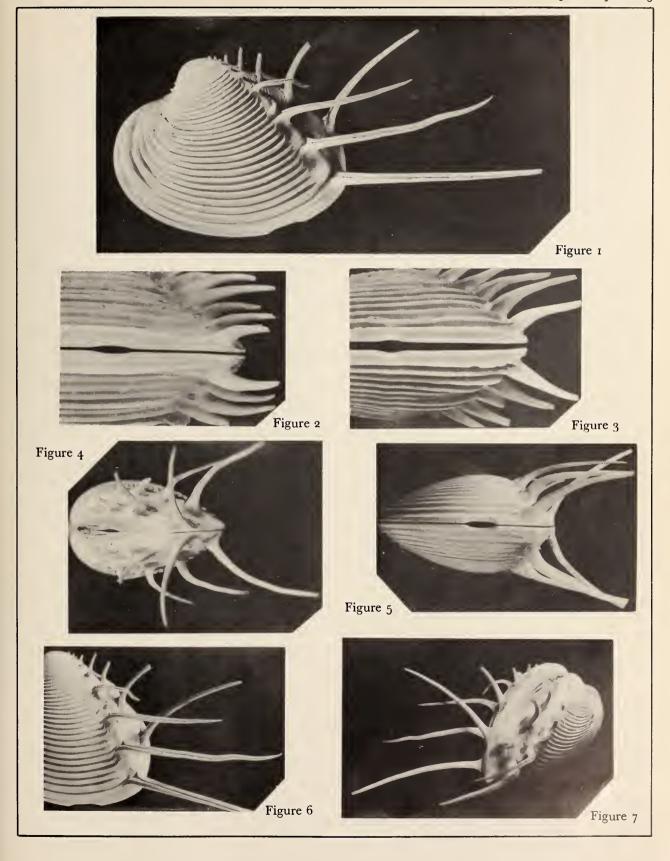
Explanation of Plate 5

Figure 1: Pitar (Hysteroconcha) lupanaria (Lesson, 1830), x 2; Recent, America; Saul Collection, Zoology Department, University of Cambridge. The left valve of a pair; note especially the rounded concentric ridges, raised at the anterior end of the shell.

Figure 2: Pitar (Hysteroconcha) dione (LINNAEUS, 1758), x 2; Recent, America; Sedgwick Museum Recent Mollusca Collection, Cambridge University. In this, and the specimens figured as 3 and 5, note the characteristic position and morphology of the muricid gastropod boring. Figure 3: P. (H.) dione (Linnaeus), x 2; Recent, America; Saul Collection.

Figures 4 to 7: P. (H.) lupanaria (LESSON), x 2; Recent, America; Saul Collection. A beautifully preserved double-valved specimen, photographed from varying angles to show the arrangements of the spines. Note particularly that no protection is afforded by the spines to guard the posterior gape against turbid sediment.

[The magnification is stated approximately for all figures]





primary row) carried on the rounded posterior carina delimiting the edge of the corcelet', and the other (the secondary row) along the shell sector marking the edge of the escutcheon.

ECOLOGY

Hysteroconcha is collected living on sandy beaches, and also offshore to depths of about 13 fathoms (Keen, 1958). Mr. J. Q. Burch (personal communication) has collected it living on sandy beaches near Guaymas, Sonora, Mexico. He comments that it is common as an intertidal form when a living ground has been located (i. e. there are large numbers of individuals), but that localities where it occurs are rare. Like many intertidal bivalves it remains buried under the sand when the tide is out, rising to the substrate surface to feed on the incoming tide. Its feeding position I thus infer to be with the posterior spines, and probably most of the corcelet, protruding above the substrate. The anterior end of the shell is undoubtedly always buried.

The only predator reported as actually feeding in the field on Hysteroconcha is Polinices reclusianus (Deshayes, 1839), which lives under the sand in the same habitat (Mr. Burch, personal communication). Other predators that are found in the same type of ecological station include muricid gastropods (Forreria, Hexaplex, Muricanthus), Natica, Oliva, asteroids (Astropecten), crabs and fish (Dr. M. Keen, Professor F. M. Bayer, personal communication).

DETAILED MORPHOLOGY

Hysteroconcha lupanaria group

[Hysteroconcha lupanaria (Lesson, 1830)] This species group can be recognised by the large size of the adult shell (up to 60 mm long, excluding spines), the possession of a large pre-spinous dissoconch (about 6 mm long) and the characteristic rounded concentric ornament (not sharp, raised lamellae) in the centre of the main disc.

The exact pattern of spine secretion is variable within all species of *Hysteroconcha*. However, an attempt is made below to describe the pattern that sets of spines on the majority of animals approximate to; it must be stressed that this involves considerable generalisation, and that

it will be possible to find an animal for which just about every statement made below is mildly incorrect.

Spines

On any one valve the first spine secreted in ontogeny is generally of the primary row, and thereafter spines are secreted at regular intervals alternately on the primary and secondary spine rows. On a particular spine row, say the primary, though the spines are definitely secreted on a regular pattern, the distance between any two consecutive spines increases during life, *i. e.* the ontogenetically earlier spines are closer together than the later adult ones.

The pattern of spine arrangement between the two valves is also variable, but generally the spines of the two primary rows are secreted alternately, whilst those of the two secondary rows are introduced in symmetrical pairs at the growing edge (Plate 5, Figures 4, 5, 7). However, not uncommonly the spines of primary and secondary rows are both introduced as symmetrical pairs at the growing edge. Irrespective of this, the alternating relationship between spines on the primary and secondary rows of one value is generally maintained (Plate 6, Figure 8).

The spines of the primary row rise from the valve edge at a fairly high angle in an almost truly radial direction (Plate 5, Figures 5, 6). However, they quickly become directed posteriorly, at the same time bending markedly into subparallelism with the plane of the commissure. They may achieve a length the same as, or a little longer than, the shell length at the time of their inception (e.g. spine length 34 mm, shell length 27 mm).

The spines of the secondary row rise from the shell edge at a very high angle (over 80°), and are slightly directed posteriorly from a true radial direction (Plate 5, Figures 4, 7; Plate 6, Figure 8). They also bend inwards toward the plane of the commissure, but much less slowly than do the spines of the primary row. As a consequence, at about half their normal length they meet with, and pass through, the plane containing the spines of the primary row (Plate 5, Figure 5). The length of the secondary row spines is normally less than the fully developed spines of approximately the same growth stage on the primary row, but they may grow to as much as $\frac{2}{3}$ of the length of the shell.

The spines themselves (that is, apart from their length and orientation relative to the valve surface) are of identical morphology in both primary and secondary spine rows. They are rounded and smoothed on the commissural side, and reflected at the edges so that a marked groove or channel runs the length of the upper surface of the spine (Plate 6, Figures 8, 10). The upper surface of the spine carries typical shell surface growth striae; they taper gradually to an extremely acute point. Even in the juvenile they are relatively thick at the base, and hence strong,

¹ The term "corcelet" is used in this paper for a morphologically differentiated area lying outside the escutcheon at the posterior end of the shell. A further discussion of the term may be found in Carter, 1967.

for the size of the shell (e. g. Plate 5, Figure 5). For instance in a shell 30 mm long, the last secreted primary spines are 2.1 mm thick at the base, tapering to a fine point over a spine length of 33 mm. In the largest adults that I have seen the spines are generally relatively shorter than this, but obviously extremely strong. For example in a specimen 50 mm long, the latest formed spines are only 24 mm long, but are 3 mm thick at the base: they therefore taper relatively rapidly.

Concentric lamellae

These are only developed at the anterior end of the shell in the form of flaring, recurved, sharp concentric rings, sometimes as much as 3 mm high. As they are traced across the main disc they grade insensibly into low, irregular, rounded concentric rings; in mature specimens they may become completely obsolescent just anterior to the posterior carina.

Hysteroconcha dione group

[Hysteroconcha dione (LINNAEUS, 1758)]

This species group can be recognised by the small prespinous dissoconch (about 3 mm long), the correspondingly smaller size of the adult shell (commonly less than 50 mm long), and the possession of sharp raised concentric lamellae over the whole of the main disc, and not just confined to the anterior end.

Spines

The morphology of the individual spines is much the same as in *Hysteroconcha lupanaria*, but the following minor differences in arrangement and morphology appear to be relatively consistent.

1. On any one valve the first spines secreted in ontogeny are generally coincident in the primary and secondary spine rows.

2. The spines are relatively more numerous (compare Plate 5, Figures 2 and 5); there are therefore fewer concentric laminae between each consecutive pair of primary row spines.

3. The spines are relatively shorter (for example, primary spine 14 mm long in a 28 mm long shell), broader at the base (as much as 4.5 mm wide in a 34 mm long shell), and more markedly flattened than in *H. lupanaria* (Plate 6, Figure 9).

4. Each spine is very clearly a continuation of a concentric growth element.

5. There is a tendency for the secondary spine row to have alternating introduction of spines on the two valves, and for the primary row to have paired spines (Plate 6, Figure 9).

A morphological detail especially marked in *Hysteroconcha dione*, but also present in *H. lupanaria*, is the cessation of the secondary spine row at a particular growth stage (Plate 6, Figure 9). This is generally when the shell has reached a length of about 20 to 30 mm. In some specimens an initial cessation at this shell size may be followed by a final pair of secondary row spines being secreted after a considerable gap. For instance, in one specimen the initial cessation came at about 20 mm, but there is another well developed pair of spines secreted at a shell length of 38 mm.

Concentric lamellae

The whole of the main disc between the carina carrying the primary spine row and the lunule is ornamented with spaced raised concentric lamellae, often slightly recurved dorsally. Each lamina is about 0.6 mm thick and perhaps 2 mm high; the anterior end of a lamella is markedly flared, and the distance between the shell surface and the lamina top may then be over 3 mm (Plate 5, Figure 1). The pre-spinous dissoconch does not have

Explanation of Plate 6

Figure 8: Pitar (Hysteroconcha) lupanaria (Lesson), x 3½. Same specimen as figures 4 to 7. An enlarged view of the primary spine row; note the comparative regularity of spine secretion with respect to the concentric ornament; generally any two spines are separated by 3 to 4 concentric ridges.

Figure 9: P. (H.) dione (LINNAEUS), x 3; Recent, America; Saul Collection. The primary (outer in this view) spine row delimits the edge of the corcelet; inside this are two further differentiated areas, conveniently termed the inner and outer escutcheon as both correspond to the growth tracks of particular parts of the dentition.

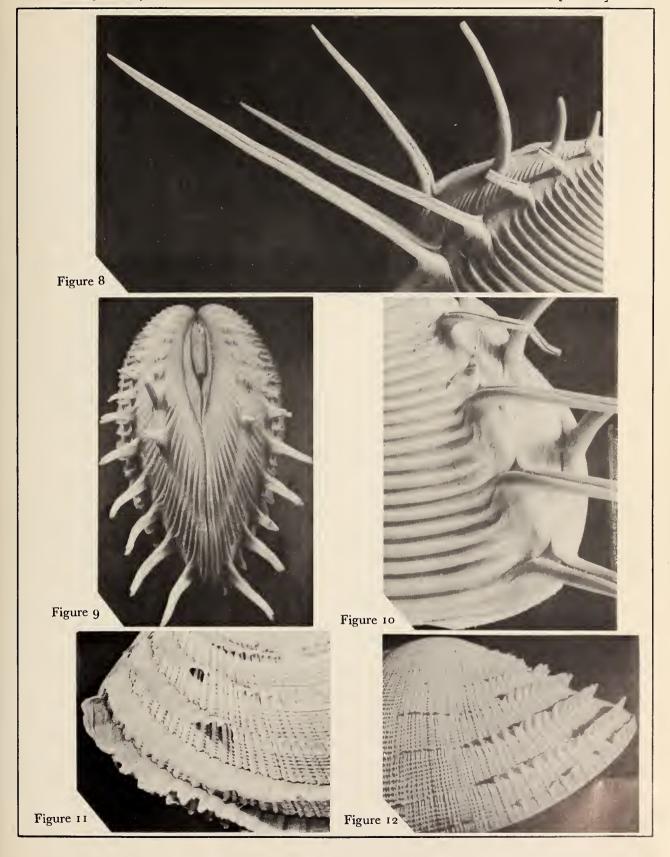
Figure 10: P. (H.) lupanaria (LESSON), x 4. Same specimen as fig.

8. Note the 'umbra' zone dorsal to each primary row spine. This zone carries growth lines clearly displaying that an epithelial tongue continued to secrete the spine after it had become displaced dorsally from the growing edge of the shell.

Figure 11: Hecuba scortum (LINNAEUS, 1758), x 5; Recent, Indo-Pacific; Saul Collection. View of the frills from a dorsal aspect showing the shallow, though marked, radial gutters, and their correspondence with the radial ornament.

Figure 12: *Hecuba scortum* (LINNAEUS), x 3. Same specimen as figure 11. View of the frills from ventral aspect. Note the structural frill ribs – each of which corresponds to a radial gutter on the dorsal surface of the frill (cf. fig. 11).

[The magnification is stated approximately for all figures]





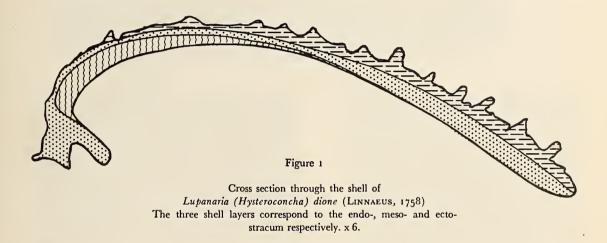
raised lamellae, though it does have low rounded concentric ornament. There may also be faint concentric ornament on the corcelet and escutcheon (Plate 6, Figure 8).

SHELL STRUCTURE

Macroscopically a section through the shell reveals the characteristic three shell layers, each clearly marked by its differing texture (Text figure 1). The ectostracum is

stracum. They are clearly due to a periodic extension of the mantle beyond its normal shell edge limits, but secretion continues unchanged during these periods of mantle extension.

The boundary between the ectostracum and the mesostracum is gradational; there is a gradual fading away of the crossed lamellae into the mesostracum. The mesostracum itself is composed of thin subparallel laminae and carries many conspicuous secretion traces; it is otherwise microscopically structureless.



white, with pink tinges near the shell surface, and clearly composed of crossed-lamellae of calcite. The mesostracum is structureless but has a very characteristic grey 'greasy' appearance like that of nepheline. The endostracum is a light grey-white, and coarsely layered.

Microscopically (Text figure 2) the ectostracum is made up of fairly coarse crossed lamellae – a large lamella being about 0.05 mm wide at its thickest point – which are always at right angles to secretion traces, and thus clearly reflect the actual direction of shell secretion. Bundles of crossed lamellae are terminated ventrally by strong secretion traces; these presumably represent growth pauses of greater or lesser extent. The individual calcite folia can often be traced across these secretion traces, but the fact that this is not always so – sometimes there is a completely new and unrelated set of folia initiated on the ventral side of the trace – lends credence to the suggestion that the traces represent extended growth pauses. The individual folia are noticeably finer on the inner side of the ectostracum.

The raised concentric ridges on the shell surface, and therefore the spines, are entirely built of ectostracal shell material that is identical with that of the main ectoThe endostracum coincides with the area of shell inside the pallial line, and abuts sharply behind the dentition (Text figure 1). It is microscopically very similar to the mesostracum, but it is clearly separated from that layer by the thin pallial myostracum. There do not appear to be any shell canals [sensu Omori & Kobayashi, 1963; tubule (Oberling, 1964) is already in use for a part of the stomach diverticula].

INFERRED PATTERN OF SHELL SECRETION

There is a certain rhythmical activity in the mantle edge of *Hysteroconcha*, similar to that in many less striking venerids, which results in the secretion of concentric shell ornament. The activity takes the form of the extension of a narrow strip of mantle beyond the general shell edge, and its reflexion to make an angle of about 60° with the plane of the commissure. Whilst in this relatively exposed position outside the shell, the mantle secretes a layer of shell about 0.6 mm thick. Generally the extended mantle strip stretches from the edge of the lunule to the primary spine row and thus the result is raised concentric lamellae of similar disposition.

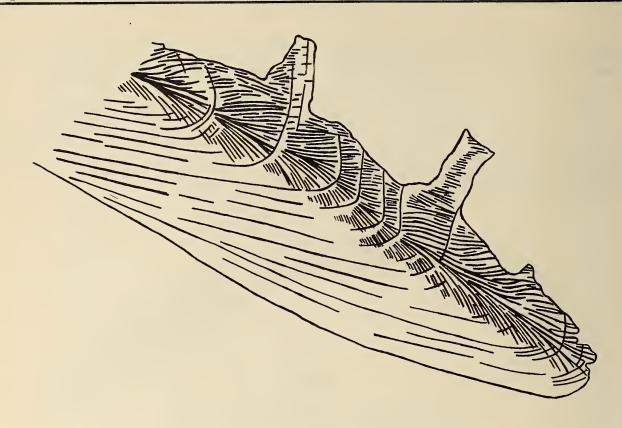


Figure 2

Enlarged view of the valve edge (x 30) showing only meso- and ectostracum. Note the gradational boundary between the two layers, the fact that the concentric lamellae are constructed entirely of ectostracum, and the fact that the crossed calcite lamellae of the ectostracum record the actual direction of shell secretion at any point.

Upon this basic pattern is superimposed another: about every third mantle expansion a small tongue of mantle at the posterior end of the raised mantle strip starts to expand locally, secreting as it does so. This local expansion is presumably caused by localised mantle cell generation. The result is the gradual building of

a projecting spine of calcareous material, smooth underneath (analogous to the normal internal shell surface), but bearing above the typical growth lines and microornament of the external shell surface. The tongue of mantle continues to expand, all the time secreting and closely adhering to the spine that is resulting. The edges

Explanation of Plate 7

Figure 13: *Hecuba scortum* (LINNAEUS), x 2; Recent, Indo-Pacific; Saul Collection. Right valve of a pair, showing the general morphology, and an unsuccessful gastropod boring.

Figure 14: H. scortum (LINNAEUS), x8; Recent, Indo-Pacific; Saul Collection. Enlarged photograph of the posterior spine row; note the pointed nature of the spines and the presence of a dorsal keel.

Figure 15: H. scortum (LINNAEUS), x 4. Same specimen as figure 14. Muricid predation localised on the mid-ventral border (cf. figs. 2, 3 and 5).

Figure 16: Spondylus spec., x 3; Recent, unlocated; McAndrew Collection, Zoology Department, University of Cambridge. Photograph of the under side (i. e. the side facing the opposing valve) of a major spine. All the spines on this specimen have expanded tips that one might suggest as paradigmatic for sensory mantle protection (N. B. This is only taken as a convenient example; I am in no way implying that the spine figured should be so interpreted).

Figure 17: H. scortum (LINNAEUS), x 3. Same specimen as figure 15. General view of the corcelet, and spine bearing posterior ridges.

[The magnification is stated approximately for all figures]

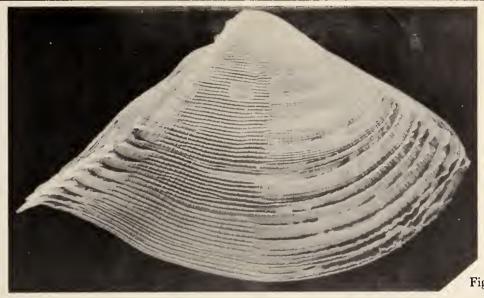


Figure 13



Figure 14



Figure 15



Figure 16

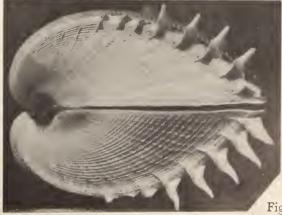


Figure 17